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REVIEW OF PLANT ELEVATION CHANGES IN ARIZONA

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ABSTRACT

A recent paper (Brusca et al. 2013a) reported dramatic elevation range changes for 27 plant species in the Catalina Mountains of Arizona in the 50-year interval following Robert Whittaker and William Niering's vegetation studies in the early 1960s. Brusca et al. interpreted these differences as responses to climate change, but while the observations by Brusca et al. are consistent with what might be expected with a changing climate, correlation does not imply causation. Detecting significant change requires accurate knowledge not only of the actual ranges of species but also of species abundance and distribution, at two points in time. Determining the causes of any changes identified requires knowledge of population dynamics and of ecological processes occurring during the time period studied. The commentary here reviews the purported changes in Catalina species as well as other pertinent literature by addressing three main questions: What are the actual ranges of species analyzed? How do we detect changes in them? How can we determine the cause of any changes?

Increased warming, drought, and reduced stream flows are among recent ecological changes in the southwestern United States consistent with climate change. Garfin et al. (2013) indicated there is high confidence climate-induced impacts will include continued warming, changes in precipitation regimes, and more extreme weather in the Southwest, all of which will result in significant ecological impacts. Ecological responses to climate change may include changes in phenology, physiology, range, abundance and distribution, community composition, trophic interactions, and ecological structure and dynamics (Walther et al. 2002; Root et al. 2003; Parmesan 2005). Considerable evidence has been found for species' range changes and shifts in phenology (Chen et al. 2011; Parmesan & Yohe 2003).

In "Dramatic response to climate change in the Southwest: Robert Whittaker's 1963 Arizona Mountain plant transect revisited," Brusca et al. (2013a) compared a subset of data they collected August 5–14, 2011 from 33 0.1 hectare plots (10 x 100 meters), all in upland areas located between 3,500–9,111 feet elevation in the Santa Catalina Mountains, Pima County, Arizona (the Catalinas) with data collected in 1962–1963 by Whittaker and Niering during their classic studies of the vegetation of the mountains (Whittaker & Niering 1964, 1965, 1968a, 1968b, 1975; Niering et al. 1963, 1984; Whittaker et al. 1968). A full description of the data from which Brusca et al. (2013a) drew their subset is described in Moore et al. (2013).

Whittaker and Niering (1964) summarized species and related ecological data in a multi-page table reporting species presence in "elevation belts" of 1,000-foot increments from 3,000–9,000 feet in the Catalinas. The methodology used to construct this table is described in greater detail in Whittaker and Niering (1965, pp. 432–433). Data from the Catalinas was collected in 350 0.1 hectare quadrats (20 x 50 meters). Most plots were near the Mount Lemmon highway, but an unspecified number were in Lemmon, Pine, Sycamore, Bear, Sabino, and Pima Canyons. In addition, 80 "bajada" plots were located between 2,500–3,000 feet elevation in the Catalina foothills, including the Campbell Avenue area several miles from the highway; 50 plots were located at 9,000–

10,600 feet in the Pinaleño Mountains (some 60 miles northeast of the Catalinas); and 15 plots were at 2,400–2,800 feet in the Tucson Mountains (about 10 miles west of the Catalinas). The actual locations of all of these plots, as Brusca et al. (2013a) acknowledged, are unknown, as is the species composition of the plots.

Brusca et al. (2013a) reported elevation range changes for 27 plant species along the Catalina highway, an elevation gradient of over 5,500 feet and a distance of 20 miles, in the 50-year interval and attributed these changes to climate change. This study illustrates several problems in detecting and understanding species' range changes, tasks that require answering three basic questions: What are the actual ranges of species analyzed? How do we detect changes in them? How can we determine the cause of any changes? The following discussion is intended be a brief review of selected literature addressing these three questions, not a comprehensive review of the current knowledge of species' ranges such as that found in Gaston (2003).

United States customary units of measurement are in used below to facilitate comparison with data presented by Whittaker and Niering, Brusca et al., and other resources on the local flora.

Species ranges

Patterns of species composition and diversity are influenced by four processes: selection, drift, speciation, and dispersal (Vellend 2010). Species' ranges result from the interaction of these processes. Gaston (1991, 2003) described two measures of geographic ranges: the *extent of occurrence*, the geographic spread of a species' distribution, and the *area of occupancy*, where the species is actually found. These concepts are similar to "abiotically suitable area" and "occupied distributional area" used by Peterson et al. (2011). Both extent of occurrence and area of occupancy may include interruptions in suitable or occupied habitat resulting from factors such as topographic features and dispersal mechanisms, and both may fluctuate over time. Determining extent of occurrence can help understand the factors impacting species' range limits and to identify suitable habitats; identifying area of occupancy can help understand population dynamics, including distribution fluctuations over time (Gaston 2003). Gaston and Fuller (2009) discussed five approaches to measuring species distributions in geographic ranges: focusing on marginal occurrences, habitat distributions, range-wide occurrences, statistical modeling, and process-based modeling. They indicated that the most accurate estimates of extent of occurrence are obtained by using marginal occurrences, while the best estimates of area of occupancy are based on range-wide occurrences.

Species are neither evenly nor randomly distributed but are found in spatial structures such as patches or gradients (niches) based on many factors, including climate and topography (MacArthur 1972; Legendre & Fortin 1989; Stephenson 1990; Brown et al. 1995). In mountainous regions such as the Catalinas, habitats are highly heterogeneous, not "remarkably uniform" as Brusca et al. (2013a) claimed (see Gentry 1988; Lomolino 2001). Species assemblages in the Catalinas vary widely with elevation, topography, soils, substrate, and other factors as described by Whittaker and Niering (1964, 1965, 1968a, 1968b) and Whittaker et al. (1968). Microhabitats and microclimates (see Potter et al. 2013) significantly increase habitat complexity. Ecological niches, spatial variation in habitats, dispersal capability, and phenotypic plasticity directly impact distribution and abundance (Holt 2003; Soberon & Peterson 2005; Valladares et al. 2014). Stochastic processes such as colonization, extinction, and ecological drift also alter species' ranges (Chase & Myers 2011). Although species' ranges may be in equilibrium for considerable time, they are dynamic, expanding and contracting in response to changing abiotic and biotic drivers (Sexton et al. 2009). Determining the complete distribution of species, as well as areas of highest density, can be difficult (Sagarin and Gaines 2005; Sagarin et al. 2006). The ecological importance of peripheral or edge populations, those at some distance from the area of highest density, is unsettled (Hardie & Hutchings 2010; but see Lesica and Allendorf 1995; Hampe & Petit 2005; Slaton 2014). Numerous factors may impact the dynamics of

range limits (Gaston 2003; Sexton et al. 2009; Angert et al. 2011; Woods 2014). Small peripheral populations at the limits of a species' range may have little ecological importance unless they both persist and reproduce (Hardie & Hutchings 2010). Gaston (1991) noted that species ranges do not have true edges and that including "vagrant individuals" (isolates or outliers) can significantly alter perceived ranges. Because neither Whittaker and Niering (1964, 1965) nor Brusca et al. (2013a) assessed species' distributions and abundances, the actual elevation ranges of species in their study areas, as well as the total ranges of these species, are unknown.

Detecting range changes

Determining whether an occupied range has changed over time is complicated by the dynamic nature of species' ranges and lack of comprehensive knowledge of them. The actual distribution and abundance of species are key to understanding range dynamics (Parmesan 1996; McGill & Collins 2003; Sagarin et al. 2006), but little definitive information about them may be known. The elevation ranges determined by Brusca et al. (2013a) were based on presence-absence data in a limited portion of the species' ranges. Whether data was collected at upper and lower range limits or in the center of ranges was not determined by either Whittaker and Niering (1964, 1965) or Brusca et al. (2013a). Range change assessments based on presence at range limits may lead to erroneous conclusions because the dynamics of peripheral populations may be quite different from those at the area of highest density (Hardie & Hutchings 2010). Fluctuations in a local area may have little relationship to the dynamics of the entire range (Holt 2003) and may simply reflect normal variability within ranges. Marginal occurrence (presence data collected at range limits) is not a good measure of the actual area occupied by species unless occurrences are highly aggregated (Gaston & Fuller 2009). Strayer (1999) indicated that presence-absence data is useful when seeking to detect uniform declines throughout the ranges of common species and to detect local extinctions, particularly when a large number of sites are surveyed. Such data may not be appropriate, however, when few sites are surveyed, abundance is low, survey intensity is low, if there is high spatial variability in the population, or if declines are widespread rather than concentrated (Strayer 1999). Shoo et al. (2006) found that the minimum range changes detected in species' distributions decreased with increased sampling, that differences in sampling methods between time periods resulted in systematic bias in estimates of range shifts at upper and lower range limits, and that estimates of mean altitudes were less dependent on sampling effort than estimates of range boundaries. Archaux (2004) argued that shifts in mean elevation are indicative of population responses whereas shifts in upper and lower range limits reflect individual responses. The most accurate assessments of range changes would likely be based on significant shifts in the elevation average or mode for the species (see Kelly & Goulden 2008).

Brusca et al. (2013a) initially claimed they compared data from their plots to data from 30 Whittaker and Niering plots, but nowhere in Whittaker and Niering (1964, 1965) is there any mention of "30 plots." In their Erratum, Brusca et al. (2013b) indicated these "30 plots" were instead what Whittaker and Niering called "grouped samples" of "combined data from either 5- or 10 0.1-Ha quadrats" as shown in Whittaker and Niering's (1964) Figure 1, specifically the lettered points between 3,500 feet and 9,000 feet. The caption for that figure stated it was based on 400 samples and that "points with letters indicate mean elevation and topographic position of the grouped samples." There are 44 points with letters in Figure 1, 34 (not 30) of which are found on or between lines drawn across 3,500 and 9,000 feet markers on the y-axes. In their analysis, Whittaker and Niering (1965, p. 433) stated that within each 1,000 foot elevation belt "samples were subjected to two ordinations, or arrangements of samples in relation to gradients of environmental or community characteristics." It is unclear which type of "grouped samples" was used for Figure 1, but in any case actual elevations and species compositions of all the "grouped samples" were not reported. Thus the only Whittaker and Niering elevation data Brusca et al. (2013) could have used are those derived

from species presence in the 1,000-foot elevation belts reported in the Whittaker and Niering (1964) table which are not linked to specific plots.

Tingley and Beissinger (2009) described several problems in using historical species occurrence data to assess range changes: lack of non-occurrence and abundance data, imprecision in locating where historical data was collected, differences in historical and contemporary data collection methods, the assumption that detectability is constant over time, and the possibility of false presences or absences associated with species misidentification. Non-occurrence and abundance data are lacking for the Whittaker and Niering (1964) and Brusca et al. (2013a) data sets, the location of the Whittaker and Niering sites is unknown, the methods used by Whittaker and Niering (1964, 1965) and Brusca et al. (2013a) differed, and species identification in both studies cannot be confirmed since voucher specimens were not collected for each plot. Quantitative techniques such as occupancy modeling can correct or minimize some of these problems, but avoiding bias requires "at a minimum" repeated visits within sampling periods and data from a sufficient number of sites to achieve adequate statistical power (Tingley & Beissinger 2009).

Identification of differences in the highest and lowest elevation presence of 27 "common" plant species between those reported by Whittaker and Niering in 1962–1963 and those recorded by Brusca et al. in 2011 is not evidence of range changes in the Catalinas, or even along the Catalina Highway, because of the small number and location of Brusca et al. (2013a) plots. Brusca et al. (2013a) used "common" to refer only to presence of a species in five or more plots; the term is not an indication of the abundance or distribution of these species either along the highway or the mountain range as a whole. Having studied vegetation in a major drainage in the Catalinas, during more than 1,460 field trips in over 30 years, I am very surprised that only 27 species would be found in five or more plots if these plots were at all representative of the constantly changing vegetation along the highway, particularly when this list does not include a number of abundant species found in the area. Both presence and absence of a species could be a chance occurrence, particularly when sample size is small. Small sample size also prevents determination whether individuals of selected species represent isolates, peripheral populations, or the core population. Soberon and Peterson (2005) indicated that absence data is more likely to result from lack of data or insufficient sampling than actual absence unless the data has both high resolution and density. Consequently the number of plots surveyed is crucial. Absence data from the 33 Brusca et al. (2013a) plots (about 5 per 1,000 feet elevation) is much less likely to reflect true absence than such data from the 350 plots (55–60 per 1,000 feet elevation belt) of Whittaker and Niering (1964).

It is especially problematic that Brusca et al. (2013a), unlike Whittaker and Niering (1964, 1965), did not sample riparian or xeroriparian areas characterized by permanent, ephemeral, or intermittent streams. Whittaker and Niering (1964) included plots in topographic categories described as "deeper ravines or canyons with flowing streams" and "shallower draws and lower slopes of canyons." In their table, over 40% of the species listed were found in each of these topographic areas and more than 60% were found in one or both. Plants listed in the table also include several aquatic species. Yet Brusca et al. (2013a, p. 3309) justified their use of only upland plots by the claim that Whittaker and Niering data "are sparse for riparian/'wet canyon' sites." In restricting their plots to upland areas, Brusca et al. (2013a) introduced significant sampling bias (see Chytry et al. 2014). Diversity in riparian and xeroriparian habitats is often greater than that of the surrounding uplands, and many species are found at their lowest elevation limits in them (Naiman & Dechamps 1997; Levick et al. 2008). Two canyons in the front range (southern portion) of the Catalinas, one xeroriparian and one riparian, illustrate the diversity of such systems: approximately 50% of the 1,200 taxa included in the Southwest Environmental Information Network (SEINet 2014) species list for the Catalinas has been found in the xeroriparian Finger Rock Canyon drainage, a gradient of 4,158 feet that includes less than 1% of the area of the Catalinas (unpublished personal data); in lower Sabino Canyon, a riparian area between 2,700–3,600 feet elevation, about 40% of the

taxa known from the Catalinas has been identified (Joan Tedford, unpublished data). The flora checklists for both areas are based on more than 30 years of collection and observation.

Available data on species' ranges in the Catalinas is limited because the range has been under collected, in part because of the rugged topography. Arizona herbaria specimens for the Catalinas included in SEINet do not always include elevation data, and locations may be imprecise. Available data was collected by many different individuals, using different survey methods and various means of assessing elevations, over widely different time periods for different purposes. A comparison of the elevation ranges for the 27 species analyzed by Brusca et al. (2013a) with those reported by Whittaker and Niering (1964), Bowers and McLaughlin (1987) for the adjacent Rincon Mountains; and Kearney and Peebles (1960) for the state of Arizona show considerable variation. In each case, these elevation ranges are little more than "best guesses" of the actual ranges of these species because comprehensive surveys of total ranges in the respective areas, including assessment of abundances and distributions, were not made. Whittaker and Niering (1964), for example, reported *Juniperus deppeana* Steud. (alligator juniper) in the 3,000–4,000 feet elevation belt up to the 7,000–8,000 feet belt. Brusca et al. (2013a) reported an elevation range of 5,028 feet to 7,162 feet for the species, Bowers and McLaughlin (1987) reported a range of 4,200 feet to 8,400 feet, and Kearney and Peebles (1960) reported a range of 4,500 feet to 8,000 feet. The methods for determining altitude were not reported by any of these researchers. Recently a large alligator juniper, 47 inches in diameter at the base, was vouchered in Sabino Canyon (ARIZ 416153, University of Arizona Herbarium). By plotting GPS latitude-longitude coordinates on a 7.5 minute topographic map using ArcMap, the elevation was determined to be 2,750 feet. It is conceivable this very tree was the basis for presence of the species in Whittaker and Niering's 3,000–4,000 feet belt given that some of their plots were located in Sabino Canyon.

Without accurate knowledge of the actual ranges of the species analyzed and an understanding of core and peripheral populations, real change cannot be detected. There is certainly no evidence of change in the Brusca et al. (2013a) plots because data was collected at only one point in time. The Whittaker and Niering (1964) data cannot be considered a proxy for presence-absence of species in the Brusca et al. (2013a) plots 50 years ago because the locations of the Whittaker and Niering plots are unknown and because at least some of the Whittaker and Niering plots were located in large drainages at some distance from the highway. Chytry et al. (2014) demonstrated the difficulty in using data from historical plots even when the exact location of these plots is known. They further showed that comparing data from historic and new plots in different locations is "a risky business," and stated that any results must be interpreted with "the utmost caution." Errors may include detecting change when change did not actually occur, not detecting change that did occur, and detecting change in a different direction or magnitude of the real change (Chytry et al. 2014).

Determining causes of range changes

Detection and attribution of climate change impacts is challenging and usually requires significant observation over several decades (Parmesan et al. 2011; Stone et al. 2013; O'Connor et al. 2014). Species may "follow" their ecological niche when that niche moves due to changing climate (Martínez-Meyer & Peterson 2006; Van der Putten 2012), but range changes may occur in the absence of directional environmental change (Holt 2003). Few studies have documented species' range shifts directly; rather most have inferred shifts from observations at local range extremes or from changes in species composition in a limited community (Parmesan 2007). Epstein et al. (2004) reported that in the arctic, where the most rapid warming is occurring, it may be "difficult, if not impossible" to distinguish whether vegetative responses result from climate change or climate variability without at least 20 years of field studies. Brusca et al. (2013a) concluded from their analysis of a very small number of species in a very small area that "rapid vegetation change" is occurring in the Southwest and described this change as "dramatic." This is hyperbole at best.

Relatively brief observations at two different time periods in relatively limited area is insufficient to demonstrate that real change has occurred without knowledge of climatic conditions and population demographics (time of establishment, abundance, size, age structure, reproduction, etc.) of species at their elevation limits at both points in time. Has change occurred elsewhere in the ranges of species studied? Is the change temporary or permanent? Did the change occur during normal climatic conditions or during particularly optimal or adverse conditions? Was the change due to loss or addition of a robust population or a few individuals? Was a lost population the product of opportunistic colonization during climatically favorable conditions or was it a long-established population adapted to local climate variability? These are only some of the questions that must be addressed before assessing the significance of perceived change or attributing it to any cause.

Even if Brusca et al. (2013a) had resurveyed 33 of the actual plots surveyed by Whittaker and Niering (1964, 1965) and change was documented, the causes of any perceived change cannot be determined without knowing natural and human impacts in the study area over the 50-year period (see Slaton 2014; Angelo 2014a, 2014b). Potential causes for variations in species' ranges in the Catalinas include climate variability; surface disturbances such as water and wind erosion, debris flows, and fire; interspecific interactions such as competition, mutualism, and facilitation; and human activities, such as recreation, habitat conversion, introduction of invasive species, and road maintenance, construction, or reconstruction.

Precipitation and temperature in the Southwest over the last 400 years have been highly variable (Sheppard et al. 2002; Griffin et al. 2013). Continued observation over time is essential to determine the nature and impact of this variability. Brusca et al. (2013a) used mean annual temperature and mean annual precipitation to show climate trends. This is problematic because biotic responses to both climate variability and climate change result from highly complex interactions among climatic factors (Dobrowski et al. 2013). Mean temperature and precipitation values mask seasonal differences and resulting impacts (Stephenson 1990). Obtaining a good measure of climatic variability in the Catalinas is difficult because long-term local data is not available and because precipitation and temperature are strongly influenced by the topography and elevation gradient of the mountains (Shreve 1915; Whittaker & Niering 1965). Brusca et al. (2013a) used data from the National Weather Service station at the Tucson International Airport. The station is located on a valley floor several miles from the Catalinas, at an elevation of 2,546 feet; consequently, it is likely a poor proxy for climate in the mountains, particularly at middle and higher elevations. Weather data based on the Parameter-elevation Relationships on Independent Slopes Model (PRISM) described by Daly et al. (2008) is physiographcally sensitive and is available for 1895 to present; PRISM would be a better source for approximating temperature and precipitation in the Catalinas. Seven years' data from three rain gages at 3,100 feet, 4,920 feet, and 7,250 feet in my study area in the Finger Rock Canyon drainage of the Catalinas indicate that PRISM data overestimate precipitation at lower elevations, underestimate precipitation at higher elevations, but provide a fairly accurate estimation of precipitation at middle elevations. PRISM data closely reflect the pattern (relative amount and spacing) of precipitation in the drainage and provide a far more accurate approximation of precipitation over the elevation gradient than Tucson International Airport data.

Some of the plants defining the range extremes 50 years ago may have germinated and lived for a time under optimal climatic conditions and then died when conditions returned to normal or worsened significantly. Droughts are cyclical in the American Southwest, and major droughts occurred in the early 1900s and 1950s (Sheppard et al. 2002). Since the late 1990s the area has experienced persistent drought accompanied by warmer than normal temperatures (Woodhouse et al. 2010). Drought alone could explain any changes in elevation that might have occurred in the last 50 years. When drought conditions ease, particularly if optimal conditions follow, plant ranges could expand.

Although climate variability is the most likely cause of short-term changes in species ranges, natural and human caused surface disturbances cannot be discounted. These disturbances, with the exception of non-native species invasions and major fires, are usually limited to fairly small areas, but the areas affected could have been the very plots studied by Whittaker and Niering or Brusca et al. Significant runoff during major storm events such as those that occurred in the winter of 1992–1993 and the summer of 2006 in the Catalinas may remove vegetation on steep slopes and shallow drainages and can scour riparian areas (Naiman & Dechamps 1997; Levick et al. 2008). Debris flows, commonly known as rock slides, such as those that occurred in the Catalinas in 2006 can cause extensive change on steep slopes and canyon bottoms (Youberg et al. 2008). Recreational uses such as camping or hiking can eliminate vegetation through trampling, soil compaction, or harvesting. Such uses may be of particular importance since most of the Whittaker and Niering (1964) plots and all of the Brusca et al. (2013a) plots were near the heavily traveled highway. Additionally, significant reconstruction of the highway has occurred in the last 30 years, and off-highway vehicular travel has increased.

Given high climate variability in the Southwest over the last 5,000 years (Ely et al. 1993), attributing short-term changes in average temperature and precipitation, or short-term vegetative changes of a few species, to climate change is highly problematic given both the resolution and time span of available data (Gaston 2003). As Overpeck et al. (2005) noted, "Climate variability and change during the past century have been modest relative to alterations in the climate system in the past." Vegetative communities may be relatively stable over long periods, but the composition of these communities continually changes during normal climate variability (Sexton et al. 2009). It seems highly likely that if climate change is impacting vegetative communities, there would be multiple responses over time, including changes in (a) onset, duration, and end of flowering, (b) flowering ranges, (c) species composition and structure, (d) abundance and distribution, (e) species' elevational and geographic ranges, (f) trophic mismatches, and (g) reproductive success. Moreover such changes would be expected in a significant portion of species' ranges. Identifying multiple climate-related responses over a broad area during an extended period of time would increase confidence in a conclusion that climate change is an actual driver (Root et al. 2003; Angelo 2014a, 2014b). With any degree of certainty, we can only say that short-term change in one response over a few decades is consistent with what we might expect with a changing climate.

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